

Some Observations on Caudal Autotomy and Regeneration in the Gecko (*Hemidactylus flaviviridis*, Rüppel), with Notes on the Tails of *Sphenodon* and *Pygopus*.

By

W. N. F. Woodland, D.Sc. (Lond.),

Indian Educational Service,

Senior Professor of Zoology, Muir Central College, Allahabad, India.

With 6 Text-figures.

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INTRODUCTORY.

DURING the rainy seasons (July to October) of 1914 and 1918 I made a large number of observations and experiments on the facts of caudal autotomy and regeneration in the common Indian Gecko, *Hemidactylus flaviviridis*¹ (Rüppel), a very familiar and useful 'snapper-up of unconsidered [insect] trifles' found on the walls of every bungalow in the United Provinces. In January 1915 I read a brief paper² on the subject at Madras on the occasion of the second meeting of the Indian Science Congress, but until the present year I have not had an opportunity of writing up a complete description of the results obtained by me.

The more conspicuous features of caudal autotomy and regeneration in Lacertilia, such as e.g. the intravertebral position of the cleavage or autotomy plane, the substitution of a continuous cartilaginous tube for vertebral centra, of an epithelial tube (an extension of the epithelium lining the canalis centralis) for the spinal cord, the change in lepidosis, absence of segmentation and subdivision of the muscles in the regenerated tail, and other features, have of course been known for many years (vide e. g. Fraisse³ in 1885, Brindley⁴ in 1895, and Tornier⁵ in 1897); on the other hand, judging from recent literature on the subject known to me, there still appears to be a certain amount of uncertainty respecting even some of the main facts. E.g. in Morgan's 'Regeneration'⁶ it is stated

¹ The *H. coctaei* of the 'Fauna of British India'. At least two other species or genera of Geckos are common in Allahabad, but the facts described in this paper apply to all.

² Published in brief abstract in the official account of the Proceedings of the Congress issued by the Asiatic Society of Bengal, and in several Madras daily papers.

³ Fraisse, P., 'Die Regeneration von Geweben und Organen bei den Wirbelthieren, besonders Amphibien und Reptilien', Cassel, 1885.

⁴ Brindley, H. H., "Some Cases of Caudal Abnormality in *Mabula carinata* and other Lizards", 'Jour. Bombay Nat. Hist. Soc.', vol. xi, 1897-8, p. 680.

⁵ Tornier, G., "Über experimentell erzeugte dreischwanzige Eidechsen und Doppelgliedmassen von Molchen", 'Zool. Anzeig.', Band xx, 1897, p. 356.

⁶ 'Regeneration', T. H. Morgan, 1901.

in a foot-note (p. 198) that 'the attachment of the muscles may be the cause of the break in the middle of the vertebrae, rather than between two vertebrae', and this statement (true to a large extent), coupled with Powell White's recent assertion¹ that 'there is no special autotomy-site as in the legs of crabs, but apparently any vertebra may be involved' (also true in one sense), might very easily convey the impression that caudal autotomy is a mere mechanical fracture of any given vertebra, with the connected muscles and skin. The whole truth is, as Leydig I believe first pointed out, that instead of there being only one autotomy plane as in the crab's claw, there are as many autotomy planes, each as complex in form as that of the Crustacean, as there are caudal segments. Further, I have not yet met with satisfactory accounts of the conditions under which autotomy occurs, of the exact *modus operandi* of autotomy, or of regeneration under certain experimental conditions, nor with any account of the mechanism by means of which haemorrhage is stopped when autotomy occurs, and I believe, therefore, that there is justification for describing the facts as a whole in the case of *Hemidactylus flaviviridis*.

NAKED-EYE OBSERVATIONS ON CAUDAL AUTOTOMY.

(Statement 1) That caudal autotomy is very common among Geckos may be concluded from the fact that over 50 per cent. of two hundred specimens used in my experiments bore regenerated tails, and that it is an easy process may be proved by the simple expedient of catching a Gecko by any portion of the tail posterior to the unsegmented base; thus I have caught hold of the remaining end of the tail of a young Gecko five times in almost as many seconds, and on each occasion a portion came off in my fingers. In nature the animals usually shed their tails when bitten by other Geckos or other animals (e.g. out of twelve perfect Geckos placed together in a box on one occasion five had shed their tails within an hour).

(2) Geckos never shed their tails 'spontaneously' or from

¹ Vide 'Report of Brit. Assoc. Advancement Science', Manchester, September, 1915, pp. 472, 473.

mere alarm.¹ This I have proved repeatedly by catching the animals by parts of the body other than the tail. Further, mere lateral flexion (the tail is not flexed to any extent dorso-ventrally) of the tail is insufficient to cause autotomy, as may be seen when, on being chloroformed, the animal lashes its tail vigorously. In fact, an all-essential condition for caudal autotomy is that the tail should be held a little distance posteriorly to the plane at which autotomy is to occur, a fulcrum thus being provided for the action of the muscles. I have proved this by anaesthetizing (with ether) a number of Geckos and tying cotton thread round the tail in different positions, the other end of the thread being fixed. On recovering from the ether, the captive Gecko would at first try to run away (though quite unalarmed, since I observed it from a good distance away) and only find itself a prisoner by the cotton becoming taut. It would then, after several further attempts at escape, suddenly stretch the cotton to its full extent and deliberately autotomize one segment in front of the segment held by the cotton. This autotomy was not a mere result of the longitudinal pull on the tail (it requires a considerable force to pull off a portion of the tail in the direction of its length,² though the tail can be easily broken off by sharply

¹ Gilbert White, in a foot-note on page 64 of 'The Natural History of Selbourne', states that, 'the blind-worm or slow-worm does not need a blow to induce it to cast off its tail. A sudden fright is sufficient.' This is also stated to be the case for the American *Ophiosaurus ventralis*, the 'glass snake'. If these statements be true (and the extreme brittleness of the tail is doubtless correlated with the rigidity of the tail assumed when the animal is alarmed, all the muscles contracting strongly), it is proof that autotomy is a much easier process in these forms than in the Gecko. Such forms as *Anolis principalis*, the American 'Chameleon', which can usually be captured by seizing the tail, the animal only being able to autotomize by a great effort, and *Uromastix spinipes*, which allows its tail to be pulled off rather than release its hold on its burrow, on the other hand, lie at the other end of the scale.

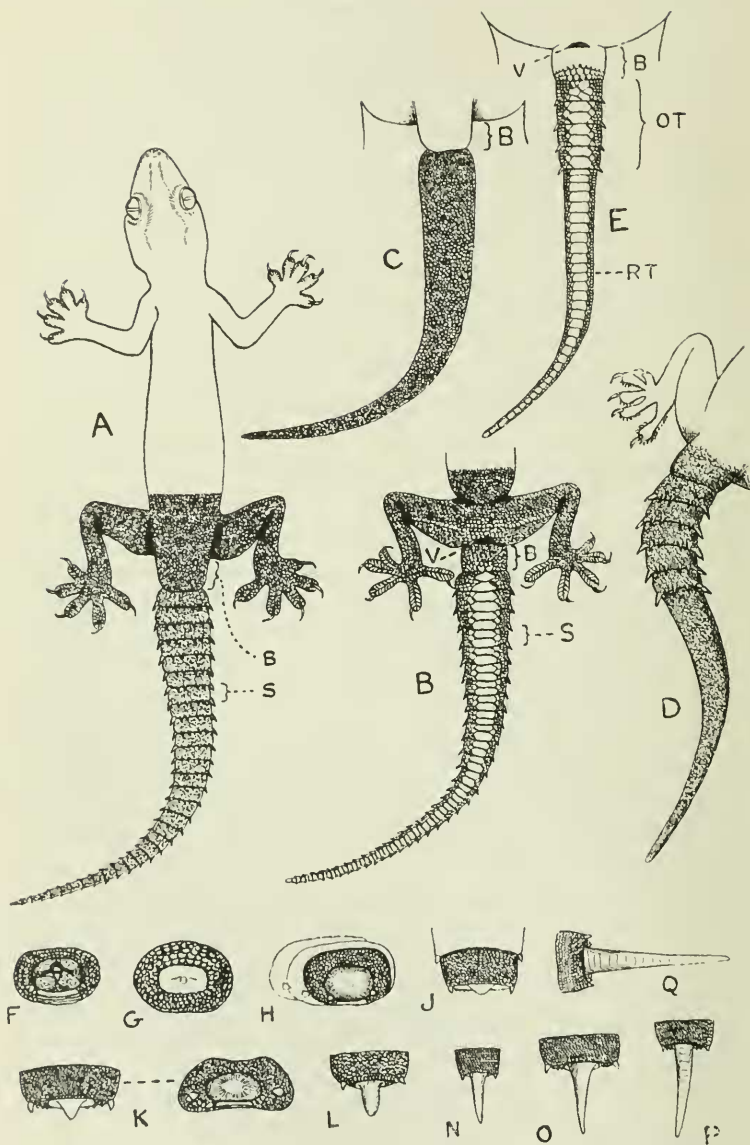
² In six recently killed Geckos, varying in length from 9.9 cm. to 13.4 cm., and in body-weight from 2.4 gm. to 5.5 gm., with the cotton thread suspending the weight tied midway in the length of the tail (hanging vertically), the weights necessary to break the original tail varied between 54 gm. and 129 gm., as kindly determined for me by Mr. B. K. Bas, M.Sc.

bending it at one point laterally), but was a result of powerful localized contraction of the tail muscles causing sudden flexion at one point. These observations prove that autotomy is a purely voluntary process, and this is confirmed by the further fact that Geckos, caught by the tail, sometimes refuse to autotomize when they perceive that escape is impossible (compare the refusal even to attempt to fill the gas bladder with more oxygen when a fish is over-weighted¹). On one occasion a Gecko, tied up by thread, remained captive for three days, though it frequently tried to run away when I approached, and it was only when I held the tip of the tail that autotomy occurred—apparently the fulcrum provided by the cotton attachment was insufficient in this case.

(3) The original (non-regenerated) tail of *H. flaviviridis* consists of a basal unsegmented region (the 'base') covered only with small inconspicuous scales, and about thirty autotomy segments, each of which can be distinguished dorsally (Text-fig. 1, A, D) by the presence on its extreme posterior edge of six large projecting scales (three on each side of the middle line), the outermost scale on each side being the largest; ventrally each segment extends lengthwise over two of the large median transversely-elongated flat scales (Text-fig. 1, B, E). As experiments prove, autotomy can occur at the posterior edge of the base of the tail or of any subsequent segment, but cannot occur in front of the posterior border of the base. In fifty captured specimens I have found examples of autotomy having occurred naturally at every segment situated between the base of the tail and the sixteenth segment: thus in seven specimens autotomy had occurred at the posterior edge of the base, i. e. the whole of the segmented tail had been shed; in ten specimens autotomy had occurred between the first and second segments, and so on, the examples decreasing in number the more posteriorly situated the site of autotomy. In nature autotomy usually occurs in the anterior half of the segmented region (Text-fig. 1, D, E), but may of course also occur posteriorly to this.

¹ Woodland, W. N. F., 'Anat. Anzeig.', Bd. XL, 1911, p. 225.

TEXT-FIG. 1.



The Gecko usually only sheds that portion of its tail necessary for escape ; in other words, autotomy usually occurs at a segment situated not more than two segments in front of the point of seizure of the tail. This is proved by the results of the following experiments :

Thread tied between	Tail shed behind
3rd and 4th segments ;	2nd segment ;
11th and 12th „	10th „
Thread tied across middle of	
8th segment ;	7th „
12th „	10th „
13th „	12th „
14th „	12th „
16th „	15th „
22nd „	20th „
26th „	25th „

TEXT-FIG. 1.

The Original and Regenerated Tails of the Gecko (all figures about natural size).

- A. *Hemidactylus flaviviridis* with original tail, dorsal view.
 B. „ „ Original tail, ventral aspect.
 C. „ „ Tail regenerated from the base, dorsal aspect.
 D. „ „ Tail regenerated from the 5th segment of the original tail, dorsal aspect.
 E. „ „ Tail regenerated from the 4th segment of the original tail, ventral aspect.

B = unsegmented base of tail ; OT = original tail ; RT = regenerated tail ; s = one autotomy segment of the original tail ; V = cloacal aperture.

- F. End-on aspect of a tail segment 3 days after autotomy has occurred. The edge of the original skin shows no sign of extension over the 'wound' surface. G. The same, 6 days afterwards. The surface of the wound is now covered over with a new young skin, formed by the histogenetic cells, hiding the transverse processes of the vertebra. H. The same, 9 days afterwards. The multiplication of the histogenetic cells has now produced a slight protuberance. J. The same, 11 days afterwards. K. The same, 13 days afterwards, dorsal and end-on aspects. The protuberance is now well marked. L, N, O, P, Q represent stages of growth after 15, 17, 19, 33, and 50 days respectively.

When a Gecko is wounded on the tail, it usually subsequently sheds the tail immediately anterior to the wound as the easiest method of repairing the injury.¹

(4) The regenerated tail, not being segmented in character (see description of structure below), cannot be shed in parts (its thin fragile extremity can, however, be easily broken or bitten off), though it may be shed as a whole either at its junction with the stump of the original tail or attached to a few segments of the original tail. This has been proved by numerous experiments which I need not record. Usually (in eleven out of thirteen experiments) when a Gecko is caught by the thick anterior portion of the regenerated tail, the whole of the regenerated tail is shed at its junction with the stump of the original tail; in some cases, however (in two out of the thirteen experiments), the regenerated tail is shed with either one or two (rarely more) of the posterior segments of the original tail attached; in other words, autotomy at the junction of the regenerated with the original tail is only a little more easy than autotomy at any ordinary joint of the original tail.

(5) Whenever autotomy occurs, the escape of blood from the caudal artery is practically nil. If, however, a segment be cut through in the middle, haemorrhage is a little more pronounced, and if the base of the tail be cut through (i. e. anterior to the first joint or autotomy plane) bleeding is profuse. The explanation of these facts will be found in the description of the structure of the original tail given below.

NAKED-EYE OBSERVATIONS ON NORMAL CAUDAL REGENERATION.

(6) Regeneration of a tail only normally occurs at the posterior surface (*a*) of the unsegmented base of the original tail, or (*b*) of a segment of the original tail, or (*c*) of the end of the regenerated tail which has had a portion broken off (not autotomized). Text-fig. 1, F-Q, shows the stages of develop-

¹ In these cases, apparently, the weakening of the joint caused by the wound renders seizure of the tail posteriorly unnecessary.

ment of the regenerated tail in *H. flaviviridis* up to that of seven weeks, and Text-fig. 5, J', K', L', shows a second tail being regenerated on the broken-off stump of a first regenerated tail.

The exact length of time it takes in *H. flaviviridis* for a new tail regenerated from the base to attain the full length of the original tail I do not know, but it is certainly not less than four or five months, and is probably more.

(7) There is apparently no limit (save that imposed by the longevity of the animal) to the number of times a tail can be regenerated.

(8) The skin of the regenerated tail is not a mere extension of that of the original tail but is a new product, as shown by both lepidosis (Text-fig. 1, D) and texture. The skin of the original tail is, like that of the trunk, head, and limbs, very soft and rubs off easily (the tail in consequence not being easy to skin), whereas the skin of the full-grown regenerated tail is relatively tough and the tail is easily skinned. After autotomy the original skin shows no signs whatever of growing over the raw exposed surface, and remains quite distinct from the new skin which covers the outgrowing regenerated tail (Text-fig. 1, H-P).

THE GENERAL STRUCTURE OF THE ORIGINAL TAIL OF *Hemidactylus flaviviridis*.

In those Lacertilia in which the tail is of distinct use to the animal for purposes other than that associated with autotomy, e.g. for prehension (as in the Gecko *Ceratolophus auriculatus*, Bavay, and in Chameleons), for swimming (as in aquatic Monitors, Iguanidae, *Amblyrhynchus*, *Lophurus*, and *Physignathus*), for steering (*Basiliscus* in water, *Ptychozoon* in air), or for balancing in air (*Draco*), caudal autotomy naturally does not occur, but it appears to me that the tail in the more common Lacertilia (Lacertidae, Agamidae, &c.) can be of but very little use to its owners. It is in these forms not used for swimming (as may be proved by throwing lizards into water,

when progression is seen to be effected mostly by undulations of the trunk, the tail only waving as an appendage of the trunk), nor for leverage (like the tails of hounds in turning corners), nor for balancing (lizards with amputated tails appear to be at no disadvantage in climbing or running), nor for means of offence (I have chased large Monitors in the jungles on the south coast of Ceylon and in southern India and on no occasion have they attempted to strike with their tails, though they can lash them); on the other hand, the tail must often be a positive disadvantage, since it is easy to catch most lizards by their tails. It is also a fact that in many lizards the tail muscles are more or less degenerate (the white muscles being valued as food in many cases), or at least incapable of exerting much force (in Central India the snake-charmers tie, without cord, the tails of small Monitors in loops round their necks, the bases of the tails then serving as convenient handles!).

These being the facts, it is not surprising that numerous Lacertilia have discovered in their tails, otherwise useless and indeed a danger, a means of self-preservation by the adoption of caudal autotomy. As we shall see in the Gecko, the whole structure of the tail is adapted for autotomy at every joint, and if, after describing these adaptations, we glance at the structure of the tails of lizards which are non-autotomous (e. g. *Calotes*), we shall appreciate the considerable simplification of structure which must have taken place in the ancestors of the Gecko in order to produce an autotomous tail.

If we examine longitudinal (Text-fig. 2, A, C) and transverse (Text-fig. 2, B) sections of the original Gecko tail we shall observe the following features. (*a*) The skin is divided into cylindrical regions, each covering one complete autotomy segment, by lines of cleavage (described in detail later), each of which extends round the entire circumference of the tail, and the small scales forming the uniform covering of the skin are arranged (Text-fig. 2, A) in correspondence with these regions: at the anterior or posterior edge of the region bordering the line of cleavage the small scales are arranged in a transverse circumferential line, whereas in the space between the lines

of cleavage, the scales of adjacent longitudinal rows alternate with each other. (b) Underlying the skin is a layer of fat cells, thin dorsally, thick laterally, and extremely thin ventrally (Text-fig. 2, B). This subcutaneous fat layer of the tail is also divided into cylindrical segments by lines of cleavage continuous with those of the skin; on their internal surface the fat cells are bounded by a thin dense layer of connective tissue. Text-fig. 3, K represents the fat layer which has been cut through in the mid-dorsal line and flattened out. The extreme thickness of the two laterally-situated regions is well shown. (c) Lying internally to the subcutaneous fat layer is a layer of muscles, the caudal flexor muscles, the attachments of which will be described later. The laterally-situated flexor muscles are the thickest, as might be expected. On their external surfaces these muscles abut against the dense connective tissue lining of the subcutaneous fat layer, and on their internal surfaces they are for the most part attached to the outer surfaces of the submuscular fat bands. (d) Lying internally to the layer of caudal flexor muscles are the submuscular fat bands. These thick bands are four in number, two on each side of the vertebral column, and on each side one lying dorsally to the transverse process of the vertebra and the other ventrally. These fat bands are, like the subcutaneous fat layer, chiefly composed of fat cells, and are segmented by lines or rather planes of cleavage continuous with those already mentioned. The four fat bands are traversed by eight longitudinal radiating connective tissue septa (one dorsal, one ventral, two lateral, and four in between these), which unite the dense connective tissue layer lining the internal surface of the fat layer with the thin layer of connective tissue investing the vertebral column. These and minor septa (shown in Text-fig. 3, J, in which the fat layer has been cut through along eight lines, and the muscles and skin removed) separate the individual muscle processes from each other and serve to some extent for the attachment of the muscles. (e) Internally to the submuscular fat bands and forming the axis of the tail is the caudal vertebral column.

Each elongated saddle-shaped vertebra consists of an elongated centrum containing a notochordal canal (full of tissue not shown in the figures) running continuously between successive centra but closed at the planes of cleavage (autotomy planes), to be mentioned shortly. Successive centra are separated by intercentral pads of cartilage (perforated by the notochord), to which the bony haemal arches (chevron bones) are attached below. Midway in its length, and on the anterior side of the vertebral cleavage plane, each centrum gives off laterally on each side a large transverse process, which extends outwards and posteriorly to the outer surface of the submuscular fat bands. On the ventral side of each intervertebral joint and attached to the joint (not the centrum) is the haemal arch which bears a median haemal spine for the attachment of muscles. Dorsal to the centrum is the neural arch which mid-vertebrally bears a conspicuous neural spine. The well-known feature of the vertebral column in the segmented region of the tail is the presence of a vertebral cleavage plane dividing the whole vertebra (centrum and neural arch) into two pieces in the middle of its length, each autotomy segment thus containing the two halves of two successive vertebrae. This vertebral cleavage plane is marked by a hyaline septum which is continuous with the similar septa marking the cleavage planes of the skin, subcutaneous fat layer, muscular layer, and the submuscular fat bands, and it is therefore obvious that, with the exceptions of the spinal cord, spinal nerves, caudal artery, and caudal vein, and certain longitudinal blood-vessels, the whole substance of the tail is traversed at each intersegmental joint by a hyaline septum marking a continuous cleavage plane.

Nor do the adaptations to autotomy in the various systems of organs cease here. Though naturally the spinal cord and small longitudinal nerves and blood-vessels show no signs of cleavage planes, yet when we examine the two big blood-vessels of the tail we find special mechanisms for stopping haemorrhage when autotomy occurs. (f) The caudal

artery, when observed in longitudinal (Text-figs. 2, A, C, and 3, P) and serial transverse sections, is seen to possess in its course a number of regions in which its walls are very thick and its lumen therefore small. These thick-walled small-lumened regions constitute sphincters for the closure of the artery lumen, and each one of these sphincters is found to be situated immediately anterior to an autotomy plane (and behind the haemal arch of each vertebra) in the region of autotomy, and there is also one in front of the first autotomy plane (behind the last haemal arch of the unsegmented base of the tail), as might be anticipated. When autotomy occurs at any segment it is the closure of the sphincter on the caudal artery immediately in front of this segment that prevents haemorrhage. As far as I am aware, this is the only instance yet described of a sphincter muscle being developed on a blood-vessel. (g) The caudal vein does not possess sphincters and this is not surprising, since the flow of blood is towards the body and therefore away from the portion of tail which is cast off. Nevertheless, to prevent undue loss of blood when autotomy occurs, the vein becomes constricted in the region of each plane of cleavage and dilates at each in-between region (Text-fig. 2, A, C), i. e. in the region of each haemal arch, and when the tail is shed the open lumen apparently becomes temporarily plugged up by blood-clotting. (h) Concerning the spinal cord there is nothing worth remarking, save perhaps that it contains as usual Reissner's fibre (I have also observed this in the tail of *Pygopus* which is autotomous). It maintains an approximately uniform diameter throughout its course. On the ventral side of the spinal cord and in contact with its substance is a subneural vessel; also contained in the neural arch but lying external and ventral to the spinal cord are usually to be seen two lateral neural vessels, which in reality are part of a plexus of blood-vessels.

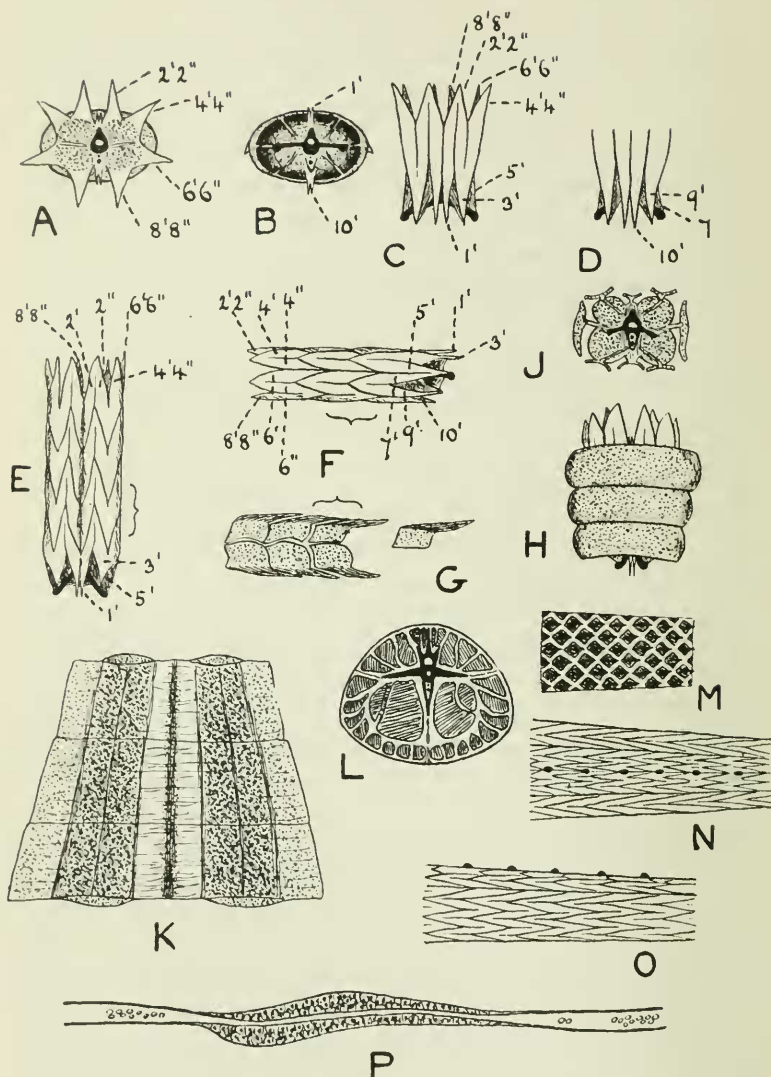
The above-named structures are to be found in the segmented portion of the original tail of the Gecko. There remains for description the unsegmented base (Text-fig. 2, A) of the tail. The

skin and subcutaneous fat layer in this region are unsegmented. The submuscular fat bands are absent, their position and that of the muscles of the tail segments being occupied by large longitudinally-disposed masses of muscle doubtless concerned with the occasional movements of the tail base. The type of muscles found in the segments of the tail is quite absent. In the base, i. e. the region between the cloacal aperture and the first autotomy plane (marking the anterior border of the first segment), two and a half vertebrae are to be found in the adult Gecko (I found three and a half vertebrae in the base of a young Gecko), and the base thus consists of the equivalents of two and a half tail segments. Only two haemal arches are present in the region of the base, these being attached to the last two intercentral cartilages, the first intercentral cartilage only possessing, like the trunk vertebrae, a small ventral nodule of bone.

THE CAUDAL FLEXOR MUSCLES: THEIR ATTACHMENTS AND MODE OF ACTION IN AUTOTOMY.

If we catch a Gecko by its original tail and examine the front aspect of the piece shed, we see (Text-fig. 3, A) that lying external to and arising from the four submuscular fat bands are eight projecting muscle processes (numbered 2' 2", 4' 4", 6' 6", 8' 8" on each side of the segment), two arising from each fat band. If we examine the hind aspect of the portion of tail left attached to the animal (Text-fig. 3, B) we again see the four fat bands, external to which are eight cavities which, before autotomy, lodged the eight muscle processes just mentioned; there are also to be seen two pairs of small tapering muscle extremities, one in the mid-dorsal line (labelled 1') and one in the mid-ventral line (labelled 10'). The transverse processes of the vertebra are also conspicuous. If we now remove from a single shed segment of the tail the skin and the subcutaneous fat layer, the entire musculature of the segment becomes visible (Text-fig. 3, C). Anteriorly the eight muscle processes are to be seen; posteriorly each of the four dorsal processes is seen to bifurcate, the halves of each, however, uniting with adjacent halves, except in the case of the two

TEXT-FIG. 3.



dorsalmost halves which are separated by the vertebral neural spine, to form altogether six posterior muscle extremities. Each of the four ventral processes (Text-fig. 3, D) end posteriorly in a similar manner. Thus on the posterior side of the segment there are altogether ten points of termination of the muscles instead of sixteen, since twelve of these fuse together in pairs and only those in the mid-dorsal and mid-ventral lines persist separately. Text-fig. 3, E, F illustrates respectively dorsal and lateral views of the musculature of several adjacent segments, from the latter of which it will be seen that the lateral posterior processes, which contract most vigorously in tail flexion or autotomy, become attached to the strong pro-

TEXT-FIG. 3.

Structure of the Original Tail of the Gecko and of the Tail of Calotes.

A. Front end-on aspect of the piece of separated-off tail after autotomy ($\times$ cir. 2). Eight large muscle processes are seen which were, before autotomy, lodged in the eight interseptal recesses seen in fig. B. B. Posterior end-on aspect of the stump of the tail after autotomy ($\times$ cir. 2). Eight recesses (situated under the subcutaneous fat layer) are visible, separated from each other by radiating septa of connective tissue: these lodged the eight muscle processes seen in fig. A. The transverse processes are visible, also the extreme hind end of the haemal process. C. Dorsal aspect of the flexor muscles of a single tail (autotomy) segment ($\times$ cir. 2). D. Ventral aspect of the posterior flexor muscles of a single tail segment ($\times$ cir. 2). E. Dorsal aspect of the arrangement of the flexor muscles ($\times$ cir. 2). F. Lateral ditto. G. Attachment of the flexor muscles to the fat bands seen in longitudinal sections ($\times$ cir. 2). H. The segmented subcutaneous fat layer exposed after removal of the skin from three of the tail segments ($\times$ cir. 2). J. Transverse section through the posterior half of a tail segment showing the central septal attachments of the fat layer. The spaces between the (cut) fat layer and the fat bands are empty and form the eight recesses referred to in figs. A and B. In the anterior half of a tail segment the fat layer is attached all round to the outer surface of the flexor muscles. K. The fat layer of three segments cut through in the mid-dorsal line and spread out. Very few fat cells are present in the thin mid-ventral area ($\times$ cir. 3). Lines of cleavage are visible. L. Transverse section of the tail of Calotes ($\times$ cir. 3). The multiple subdivision of the peripheral muscles and the absence of a fat layer and fat bands are noteworthy. The large internally-situated muscles run longitudinally the whole length of the tail. M. Portion of dorsal skin of the tail of Calotes ($\times$ cir. 2). N. Dorsal aspect of muscles of tail of Calotes after removal of skin ($\times$ cir. 2). O. Lateral ditto. P. Sphincter on caudal artery of Gecko seen in longitudinal section (magnification unrecorded, but about 70 diameters).

jecting transverse processes of the vertebra. I have labelled each of the anterior muscle processes and their posterior extremities in order that the muscle masses shown in the figure of the transverse section of a segment (Text-fig. 2, B) may be compared with those of Text-fig. 3, A, C, D, E, F. In short, dissection and serial sections show that all the posterior continuations of the eight anterior muscle processes are firmly attached posteriorly to the vertebral axis, directly dorsally and ventrally to the neural and haemal spines respectively, and laterally to the transverse processes, and indirectly by connexion with the eight radiating septa of connective tissue which join the connective tissue internal lining of the fat layer with the connective tissue external investment of the vertebrae—these traversing the area of the fat bands. The muscles are also firmly attached on their inner surfaces to the fat bands (Text-fig. 3, G), which themselves are firmly connected with the connective tissue investment of the vertebrae. The eight anterior muscle processes, on the other hand, are only feebly attached to the septa separating successive muscle segments. Usually the tail of a Gecko merely depends from the body, but when the animal is excited (as when pursuing a fly) the tail can be slowly flexed from side to side. During these lateral flexions of the tail the muscles of many segments on one side of the tail contract and the strains on the slender anterior attachments of the muscles are relatively slight, however violent the flexion (as when the animal is being chloroformed), because the muscles of many segments are involved, i.e. the effect is distributed between them and the tail is freely movable. On the other hand, when the tail is seized by another Gecko, the part of the tail seized is relatively fixed, and since the body is also fixed in position, and the muscular contraction involved in autotomy is limited to one segment (see Statement 2) and is therefore proportionately violent, the contraction of the muscle, in trying to flex relatively inflexible segments, i.e. in trying to cause to approach each other the sides of two adjacent segments which, under the conditions, can only approach to a very small extent, is then

and only then able to effect the disruption of the feeble anterior attachments of the muscles. Disruption of the muscles having occurred on one side (and with it disruption of the skin, fat layer, fat bands, and vertebrae along their cleavage planes), the muscles of the other side of the segment contract violently in their turn and so complete the process of autotomy. This interpretation of the action of the muscles in autotomy explains why it is that the Gecko cannot shed its tail unless it is held, i.e. relatively fixed, a fact which I have already remarked upon.

A BRIEF COMPARISON OF THE STRUCTURE OF THE GECKO TAIL
WITH THAT OF THE TAIL OF A NON-AUTOTOMOUS LIZARD—
Calotes versicolor.

If we examine the tail of a typical non-autotomous lizard, such as *Calotes versicolor*,¹ we find conspicuous differences from the Gecko tail. In *Calotes* the tail is covered with equal-sized scales arranged in longitudinal rows, all the scales of adjacent longitudinal rows alternating with each other in position (Text-fig. 3, M); thus the arrangement of the scales shows no signs of segmentation, and lines of cleavage are of course absent. The annular arrangement of the scales at the ends of the autotomy segments of the Gecko tail must therefore have arisen secondarily in relation to autotomy. Internally in the *Calotes* tail, fat layer and fat bands are both absent, the entire space between the skin and the vertebral column being occupied by muscles. The general arrangement of these muscles, which can be seen when the tail is skinned (Text-fig. 3, N, O) and from transverse sections (Text-fig. 3, L), is much more complicated than in the Gecko tail. In *Calotes* all the superficial muscles are arranged in a zigzag myotome fashion, but those internally situated are continuous (not myomeric) and run longitudinally the greater part or the whole of the length of the tail. In *Varanus* a similar arrangement of the muscles obtains. From these facts it will appear

¹ The cut tails of two *Calotes* showed no signs of regeneration after one and a half months of captivity, and I have never met with a regenerated tail in this animal in nature, nor in *Varanus*.

probable that in the Gecko tail the four sub-muscular fat bands must represent centrally-situated longitudinal unsegmented muscles which have degenerated into fat and become secondarily segmented for autotomy. It is also certain that the superficial muscles of the Gecko tail have become secondarily simplified and segmented in relation to autotomy.

PLANES OR LINES OF CLEAVAGE IN AUTOTOMY.

The annular lines of cleavage in the skin are indicated (1) by the arrangement of the scales in the skin, a regular straight transverse row of scales bordering each side of the line of cleavage (Text-fig. 2, A), and (2) by the presence of a line of very thin transparent substance, devoid of pigment and other cells, separating the two straight lines of scales of adjacent segments. Apparently in this line of tissue the epidermis and dermis of the integument have become extremely attenuated and practically reduced to a layer of non-cellular hyaline matrix, only occasionally traversed by capillaries and nerves passing from one segment to another. In the subcutaneous fat layer (Text-fig. 4, E) the lines of cleavage are denoted by similar lines, alone composed of this non-cellular hyaline matrix and bordered by several rows of connective tissue cells, outside which lie the cells of the fat layer. Similar sheets of matrix separate the muscle segments of the tail and the segmented parts of the longitudinal fat bands (Text-fig. 2, C). With reference to the plane of cleavage dividing the middle of each centrum and neural arch, Gadow¹ (p. 494) describes this as a 'cartilaginous septum . . . which coincides exactly with the line of transverse division of the vertebra . . . where the tail breaks off and whence it is removed'. This is a mistake; the vertebral plane of cleavage simply consists (Text-fig. 2, C), like the planes and lines of cleavage already mentioned, of a sheet of non-cellular hyaline substance which is continuous

¹ The Cambridge Natural History. Volume on Amphibia and Reptiles, H. Gadow, 1909.

with those separating the other tissue of adjacent segments; also the plane of cleavage lies immediately behind the transverse process of the centrum, which is therefore not affected by autotomy and remains projecting from the posterior surface of the portion of tail retained by the animal (Text-fig. 1, F). I have verified these statements in numerous longitudinal and transverse microtome sections, also in hand-cut sections, these latter proving, in virtue of their thickness, more useful on the whole than the former.

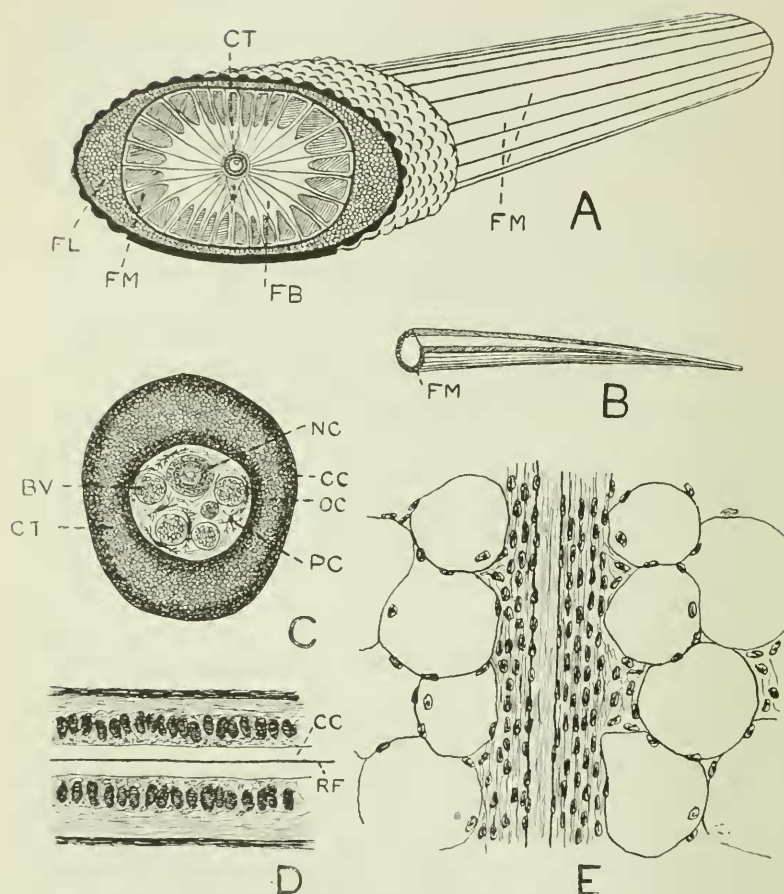
I may add here that there is apparently great general similarity between these cleavage planes in the Gecko tail and the 'breaking plane' which Paul¹ has recently described in detail in Decapod Crustacea. In fact the only conspicuous difference between the two is as regards number—in the Crustacean there is only one plane for each limb, whereas in the Gecko (as in the Ophiroid arm) there are as many planes as there are joints. And just as there is a sphincter on the Gecko caudal artery to stop haemorrhage, so in the Crustacean there is a diaphragm developed for the same purpose. In all cases muscular action affects autotomy of the shed part along the cleavage plane.

THE STRUCTURE OF THE REGENERATED TAIL OF THE GECKO.

The most conspicuous difference between the regenerated tail and the original tail is the total absence of any signs of segmentation in the former, either on the surface or in internal structure. On the dorsal surface of the tail the skin bears a uniform covering of the usual small scales (Text-fig. 1, C, D), i.e. the small scales are arranged in the same somewhat irregular manner throughout the length of the tail, and no larger scales are present. On the sides of the tail the scales are larger, and on the median ventral surface there is a longitudinal series of large laterally-elongated scales (Text-fig. 1, E). The subcutaneous fat layer is present (Text-fig. 4, A), very thin dorsally

¹ "Regeneration of the Legs of Decapod Crustacea from the Preformed Breaking Plane", J. H. Paul, 'Proc. Royal Soc., Edinburgh', vol. xxxv, 1914-15, p. 78.

TEXT-FIG. 4.



Structure of the Regenerated Tail of the Gecko.

A. Semi-diagrammatic transverse section of the regenerated tail of the Gecko ($\times$ cir. 8). The multiplication of the flexor muscles (FM) seen in transverse section (and the resulting large number of radiating septa traversing the fat bands—FB) is noteworthy, also their lack of connexion with the cartilaginous tube (CT). FL = fat layer. The caudal artery and vein are seen underneath the cartilaginous tube. B. Dissection of the fat bands and flexor muscles, showing the longitudinal course of the latter (nat. size). C. Transverse section of the cartilaginous tube ($\times$ cir. 150). BV = blood-vessel;

and ventrally and thick laterally, and as usual lined internally by a thin dense layer of connective tissue : it shows no signs of lines of cleavage, being continuous the whole length of the tail. Internally to the fat layer is the muscle layer, consisting of from twenty to thirty (in different specimens) slender muscle bands, separated from each other by a corresponding number of radiating connective tissue septa (continuations of the dense connective tissue lining of the fat layer which extend inwards through the fat band to the similar, and here thick, connective tissue investment surrounding the axial cartilaginous tube enclosing the regenerated spinal cord) and running in a straight line the entire length of the regenerated tail (Text-fig. 4, B). The fibres of these muscle bands appear to run obliquely from the central fat bands outwards to the subcutaneous fat layer and have no special connexions in their course, except that anteriorly all the bands are attached to the connective tissue septa bounding the hind ends of the muscles of the base or other portion of original tail. In autotomy the separation of the regenerated tail from the part in front of it must be solely effected by the contraction of these longitudinal muscle bands away from their connective tissue junction with the last intermuscular septum, this forcible separation causing the simultaneous separation of the slender junctions of the other organs. In other words, the tail being seized and held, these muscles contract, and since the whole body cannot be dragged back, the inevitable result is the separation of the tail.

Between the layer of muscle bands and the axial tube enclosing the regenerated spinal cord lies the substance of the submuscular fat bands already mentioned ; these are continuous from end to end of the tail (cleavage planes being

cc = calcified cartilage at periphery (the tube is also calcified on the inner edge); ct = cartilaginous tube; xc = extension of spinal cord; oc = uncalcified cartilage; pc = pigment cell. D. Longitudinal section of the spinal cord extension in the regenerated tail ($\times$ cir. 580). cc = canalis centralis; rf = Reissner's fibre. E. Section through autotomy plane in the region of the fat bands ($\times$ cir. 250). The hyaline septum is shown, bordered by connective tissue cells, outside which lie the fat cells. Similar hyaline septa extend through the vertebrae, muscles, and skin.

absent) and are radially subdivided by the numerous connective tissue septa above described. Forming the central axis of the regenerated tail is a thick-walled cartilaginous tube (Text-fig. 4, C). The cartilage of this tube is calcified¹ on its outer surface (next the fat bands) and on its inner surface (next the spinal canal), the space between these two concentric cylinders of calcified cartilage consisting of ordinary uncalcified cartilage. Anteriorly this cartilaginous tube joins on to the ring of bony tissue formed by the centrum and neural arch of the last vertebra (Text-fig. 2, C) and so secures a continuation of the spinal canal. The cartilaginous tube is quite continuous—no planes of cleavage being present—and it bears no processes of any kind, neural spines and haemal arches both being absent. The contents of the cartilaginous tube are (a) a very attenuated extension of the spinal cord (about a quarter or less of the diameter of the original) which practically consists of a continuation of the cellular lining of the *canalis centralis*, with little or none of the external nerve-fibre substance; (b) a network of capillaries which lies for the most part ventrally to the spinal cord extension; and (c) an arachnoid meshwork containing pigment cells. In view of the fact that no nerves are given off from this slender extension of the spinal cord into the regenerated tail, it is evidently quite a useless structure so far as muscular innervation is concerned; it, however, contains a well-developed Reissner's fibre (Text-fig. 4, D). It may here be mentioned that the nerves supplying the slender muscle bands are all derived from the last two or three pairs (I have not determined the exact number) of nerve roots in the stump of the original tail (according to Powell White, the nerves are, in *Lacerta vivipara*, derived from the last three pairs) and, as stated, have no connexion with the regenerated spinal cord. In the abstract of Powell White's paper it is stated that in *Lacerta viridis* the cartilaginous tube enclosing the spinal cord is 'unsegmented

¹ This calcification of the cartilage is apparent in thick unstained hand-cut sections of aceto-bichromate-fixed material; in ordinary microtome sections it is not easily seen.

and continuous except for some perforations through which blood-vessels pass to the interior'. In the fully-regenerated tail of the Gecko no perforations at all exist in the length of the tube, not even for blood-vessels, though perforations (for vessels) are fairly numerous in the young growing cartilaginous tube, and I suspect that this is also the case in *Lacerta*. It certainly is so in *Pygopus*, sections of which Professor J. P. Hill has kindly shown to me. At the extreme posterior end, however, of the cartilaginous tube in one series of sections of a fully-developed regenerated tail I have found one median ventral terminal opening and two lateral sub-terminal openings through which blood-vessels pass, but these are the only openings I have discovered. In another series of sections of a young regenerated tail (6 mm. in length) I found that the spinal cord continuation actually bifurcated at its posterior extremity, one branch piercing the cartilaginous tube through a mid-ventral subterminal opening, the other branch continuing to the end of the tube, but I suspect this to be a freak.

The caudal artery extends back into the regenerated tail lying underneath the cartilaginous tube, and only differs from that of the original tail in not being enclosed in a haemal canal and in being devoid of sphincters; it gives off branches at intervals. The caudal vein extends posteriorly under the caudal artery and is uniform in diameter.

THE HISTOGENESIS OF NORMAL CAUDAL REGENERATION.

Under this heading I can only confirm and correct previous accounts. As Powell White says, 'The wound after autotomy is quickly covered with new skin [not derived from the old skin covering the stump of the original tail], beneath which is a mass of spindle cells [quasi-embryonic tissue] which apparently originates in the connective tissue. This cellular mass acts as a growing-point to the new tail, and from it the various structures are developed. The cartilage, fat, and blood-vessels arise by differentiation from the spindle cells. The muscle fibres arise segmentally in groups, the groups nearest the tip

being the least differentiated. The muscles in the stump play no part in the process.' It is also possible that the continuation of the lining epithelium of the *canalis centralis* of the spinal cord is produced by these histogenetic cells. On the other hand, it appears that the nerve trunks of the regenerated tail are produced by the growth into the regenerating tail of the torn ends of the trunks in the original tail, the posterior root ganglia of which 'are increased in size or number owing to increase in size of the nerve bundles'. The preceding account, which I can confirm in full as regards the origin of the skin, muscles, fat layer, fat bundles, and cartilaginous tube, is thus in distinct opposition to the views of Fraisse, who believed that the skin, connective tissue, cartilaginous tube, and muscles of the regenerated tail are all derived ultimately from the corresponding tissues of the original tail—that new tissues can only be reproduced from tissues like themselves. This belief is, in the main, not only disproved by actual observation, but is also contradicted by some of the results obtained from caudal regeneration under abnormal conditions now to be described.

CAUDAL REGENERATION UNDER ABNORMAL CONDITIONS.

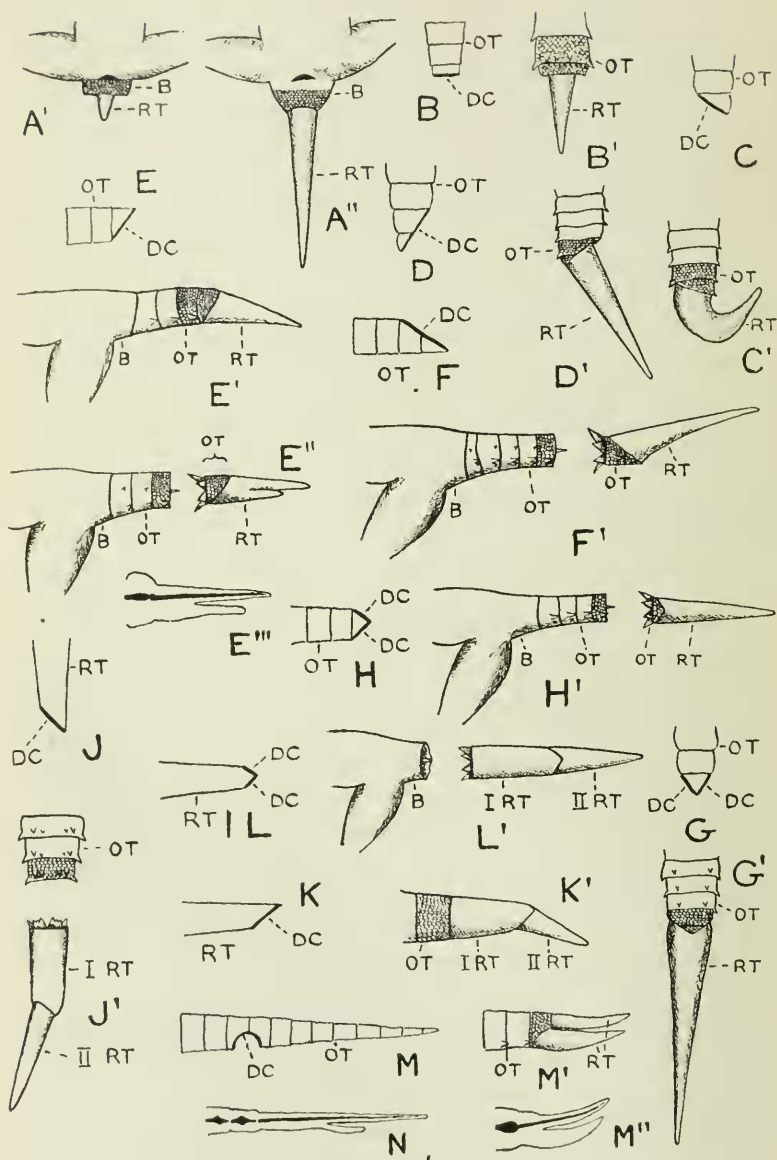
Intervertebral Regeneration. Though Fraisse rightly came to the conclusion that the remnants of the old notochord (even if these be exposed by the injury) take no part in the formation of new skeletal tissue, yet since a more recent writer like Gadow (p. 494) is of opinion that 'reproduction of centra [in the regenerated tail] is precluded by the previous normal reduction of the chorda, around which alone proper bony centra could be formed' (though Fraisse has shown that in the regenerated tail of *Urodeles* new vertebrae can be produced in the total absence of a notochord), it may be as well to quote, first of all, the results of my experiments on caudal regeneration from the posterior surfaces of caudal segments which were cut in half, i. e. cut transversely between any two autotomy planes, i. e. intervertebrally. These experiments were successful on four occasions (Text-fig. 5, B, B') and in each case, though the notochord was well

exposed by the cut, the endoskeleton of the regenerated tail was of the normal cartilaginous tube type. These experiments also prove that the tissues bordering the autotomy plane are not indispensable for the regeneration of the tail—histogenetic cells are distributed throughout the tail tissues. I may add that in one of these four experiments I held the animal by the regenerated tail (of 66 days growth) but I could not induce autotomy either from the junction of the regenerated tail with the original stump or from a true autotomy plane anterior to it.

Regeneration from the Cut Base of the Tail. I have stated that the first autotomy plane in the Gecko tail is situated between the posterior surface of the base of the tail and the anterior surface of the first autotomy segment. Since we now know that caudal regeneration can occur at the surface of any autotomy segment cut intervertebrally, i. e. between two successive autotomy planes, it is of interest to inquire whether regeneration can occur from the posterior surface of the base of the tail if this be cut through anterior to the first autotomy plane. The answer to this question is also of special interest when we reflect that the structure of the base of the tail is different in several respects from that of the segmented tail proper—in the absence of segmentation, in the absence of fat bands, and in the arrangement of the muscles—and that it has been contended that (in the Gecko and the other Lacertilia which it resembles in this respect) the regenerated tail differs in type from the original tail solely because in development the former is shut off from the controlling influence of the main organism by the hyaline septa of the autotomy planes, whereas the original tail is developed before autotomy planes (which are only produced after the original tail is formed) are present.

I performed this experiment of cutting through the base of the tail four times in 1914 but in no instance did regeneration occur, though the Geckos were kept for two months. In 1918, however, when I repeated the experiment, five of the Geckos regenerated tails of the normal regenerate type (Text-fig. 5, A', A''), as shown by the cartilaginous tube, fatty

TEXT-FIG. 5.



tissue, nerve cord, and other features seen in sections. This result is of importance because it proves (1) that regenerative cells are present in a part of the body which, under normal conditions, never reproduces a tail, and (2) that the peculiar characters of the regenerated tail are not due to mere lack of continuity with the rest of the organism. The real reason for the regenerate tail differing in character from the original tail appears to be that the organism as a whole 'knows' that the

TEXT-FIG. 5.

Experimental Regeneration of the Gecko Tail (all figures nat. size).

A'. Tail regenerated from cut base, after 20 days. A". Ditto, after 43 days. B. Diagram showing direction of cut through the middle of an autotomy segment. B'. Tail regenerated from cut-through autotomy segment (cut B), after 15 days. C. Diagram showing direction of oblique lateral cut through one autotomy segment. C'. Tail regenerated from the cut C, after 64 days. D. Diagram showing direction of oblique lateral cut through two autotomy segments. D'. Tail regenerated from the cut D, after 52 days. E. Diagram showing direction of oblique dorso-ventral cut through one autotomy segment. E'. Tail regenerated from the cut E, after 67 days. E". Tail regenerated from the cut E, after 87 days (the tail was shed when held at the point shown). E"". Diagram showing absence of endoskeleton in the lower division of the bifid tail of E". F. Diagram showing direction of oblique dorso-ventral cut through two autotomy segments. F'. Tail regenerated from the cut F, after 76 days (the tail was shed when held at the point shown). G. Diagram showing direction of two oblique lateral cuts through an autotomy segment. G'. Straight tail regenerated from the cut G, after 82 days. H. Diagram showing direction of two oblique dorso-ventral cuts through one autotomy segment. H'. Tail regenerated from the cut H, after 80 days (the tail was shed when held at the point shown). J. Diagram showing direction of oblique lateral cut through regenerated tail (cf. cut C). J'. Tail regenerated from the cut J, after 73 days (the tail was shed when held at the point shown). K. Diagram showing direction of oblique dorso-ventral cut through regenerated tail. K'. Tail regenerated from the cut K, after 73 days. L. Diagram showing two oblique dorso-ventral cuts through regenerated tail. L'. Tail regenerated from the cut L, after 73 days (the tail was shed when held at the point shown). M. Diagram showing position and extent of ventral wound made on original tail. M'. Two tails regenerated from the wound M, after 80 days. M". Diagram showing absence of endoskeleton in the lower division of the bifid tail of M'. N. Diagram showing absence of endoskeleton in the lower division of a ventral accessory tail produced from a wound similar to M, after 80 days.

B = base of tail; DC = direction of cut; OT = original tail; RT = regenerated tail.

reproduced tail is only reproduced for the purpose of being shed, and in consequence the regenerated tail is grown on cheap 'jerry-built' lines sufficient for the end in view. That this is the explanation will be clear, on the one hand, when we call to mind the regenerated tails and limbs of Urodeles, arms of Starfishes and Ophiuroids, and limbs of Crabs, Centipedes, and Plasmids (walking-stick insects), all of which, when regenerated, are required for use as integral parts of the organism and are therefore of normal type¹; on the other hand, the fact that the organism can actively mould an autotomous appendage so as to adapt it for functions not connected with its own individuality is shown in such cases as those of the hectocotylized arm of Dibranchiate Cephalopods and the heteronereis segments of Polychaetes. According to this explanation then, the aberrant scaling of the regenerated Gecko tail is to be regarded as that form of scaling most easy to be produced under the circumstances, just as the simple longitudinal muscles (devoid of connexion with the endoskeleton) and regenerated nerve cord (devoid of white matter, ganglion cells, and nerves) are to be regarded as similar products of a 'jerry-building' policy, and not due to a mere reversion-to-type tendency, as supposed by Boulenger.² The type of scaling of the regenerated tail may happen to be of an ancestral type simply because this latter chances to be a 'cheaper' or 'to-hand' form of lepidosis, but it is quite evident that since the 'reversion to an ancestral type' explanation does not apply to the internal structure of the regenerated tail, it also cannot be held to be sufficient to account for the scaling.

I may mention that previous to preserving the tail (of 45 days' growth) of one of these five Geckos, I held it with my fingers

¹ The well-known examples of an antenna being generated on the eye-stalk of *Palinurus*, of a mandible being substituted for a first antenna in *Asellus*, and a wing replacing the hind leg of the moth *Zygaena* (vide Bateson, 'Material for the Study of Variation', 1894), and other similar examples are of the same category, the 'controlling' influence of the organism as a whole, however, being at fault, the reproduced part being out of position.

² Boulenger, G. A., 'Proc. Zool. Soc.', Lond., 1888, p. 351.

and the animal shed it 'not very easily'. The stump bled to some extent, but not profusely.

Regeneration from obliquely-cut Ends of the Original Tail. When one or two segments of the original tail are cut through obliquely from left to right (Text-fig. 5, C, C') or from right to left (Text-fig. 5, D, D'), the axis of the regenerated tail is usually bent out of the straight line in order to place itself at right angles to the plane of the cut (six experiments).

When one segment of the original tail is cut obliquely ventro-dorsally and postero-anteriorly (Text-fig. 5, E, E', E'') the axis of the regenerated tail is usually bent downwards in order to place itself at right angles to the plane of the cut (three experiments).

When one or two segments of the original tail are cut obliquely dorso-ventrally and antero-posteriorly (Text-fig. 5, F, F') the axis of the regenerated tail is usually bent upwards, the more so if the number of cut segments be two (four experiments).

In four experiments in which one segment of the original tail was cut to a point by left and right lateral cuts (Text-fig. 5, G, G') the axis of the regenerated tail remained in the straight line.

In three experiments in which similar cuts were made dorsally and ventrally (Text-fig. 5, H, H') the same result was obtained.

Regeneration from the Regenerated Tail. A transverse cut through a regenerated tail merely leads to a second regenerated tail being produced (two experiments).

When the regenerated tail is cut obliquely (Text-fig. 5, J, J', K, K', L, L') the second regenerated tail behaves in the manner already described for regeneration from the original tail (at least six experiments).

Accessory Tails. In all the 1918 experiments chronicled above (which are only a selection of the experiments I actually performed), and in a number of similar experiments which I conducted in 1914, I only obtained four examples in which accessory tails were produced. Text-fig. 5, M, M' shows

the result I obtained after making a wound on the ventral surface of an original tail. In this case the tail evidently autotomized at the autotomy plane separating the two segments involved in the wound, and the surface thereby exposed produced two tails. The upper tail was a normal regenerated tail in every respect, but the larger lower accessory tail differed in the essential respect that it was entirely devoid of a cartilaginous tube (Text-fig. 5, M").

Text-fig. 5, N shows another small accessory tail produced as the result of a wound on the ventral surface of a regenerated tail. An endoskeleton was also absent in this case, as also in another similar case which I have not recorded.

In Text-fig. 5, E''' is shown a small accessory tail produced as the result of the oblique dorso-ventral cut already described (Text-fig. 5, E). The lower lobe of the bifid tail was devoid of a cartilaginous tube.

I have described these four examples of accessory tails because, to judge from the paper by Tornier, the reader might imagine that an accessory tail without a cartilaginous tube is an impossibility. This is by no means the case, as these four examples and the examples in *Anolis grahami*, described by Brindley in 1898, prove. Assuming the statements of Tornier to be correct, it would appear that the injury must reach the vertebral column in order that the accessory tail produced may contain a cartilaginous tube.

NOTES ON TECHNIQUE.

All Geckos were kept in large flower-pots, covered over with mosquito-netting, and were fed on house-flies. Tails preserved for section-cutting were fixed for 24 hours or longer in a saturated solution of potassium bichromate (100 parts), to which 5 parts of acetic acid had been added; they were afterwards washed in running water for the same length of time, and then kept in 70 per cent. alcohol until required for use. For the study of the gross structure of the tail, nothing is better than thick hand-sections (longitudinal and transverse) of the spirit-preserved material, dehydrated and mounted unstained in

balsam, the bichromate fixative acting as a stain for many of the tissues. For histology, the spirit-preserved material was first decalcified by leaving it in alcohol plus nitric acid for several weeks, and subsequently dehydrated, embedded, cut, and stained with haemotoxylin. For dissection of the muscles preliminary maceration of the tails in weak alcohol or water plus nitric acid gave good results.

NOTES ON THE ORIGINAL AND REGENERATED TAILS OF *Sphenodon punctatus*.

I have examined the original and regenerated tails of *Sphenodon punctatus* kindly given to me by Professor Arthur Dendy. The scales are arranged in the original tail in accordance with the planes of autotomy, each autotomy segment bearing dorsally one of the large mid-dorsal scales, and ventrally two transverse rows of the large hexagonal scales. The muscles, after removal of the skin, have a superficial arrangement closely resembling that of the Gecko shown in Text-fig. 3, E, F, only the muscles are more numerous. In lateral aspect, e.g., there appear to be four muscle layers (and processes) instead of two as in the Gecko (Text-fig. 3, F). In transverse section the muscles are also seen to be more numerous than in the Gecko, and they extend inwards from the skin to the vertebral column, fat bands being entirely absent. The muscles are separated from each other by thin radiating septa of dense connective tissue. I dissected out a piece of the caudal artery about 9 cm. in length and cleared it in creosote, when it was evident that sphincters were not present. The regenerated tail is of course not segmented and the scaling (irregular small scales) is quite irregular. A cartilaginous tube is present, the cartilage of which is calcified in the middle of the thickness of the ring, not on its inner and outer edges as in the Gecko. The muscles are very numerous in transverse section (about fifty bands cut across), and these are separated from the cartilaginous tube not by fat bands but by dense connective tissue, which is continuous with the subcutaneous

connective tissue by means of the radiating septa separating the muscle bands. The tails of *Sphenodon*, therefore, appear to be less specialized for autotomy than the tails of the Gecko, though the presence of definite autotomy planes, the evident simplification of the muscles, and the presence of the cartilaginous tube indicate that considerable progress has been made in that direction.

RÉSUMÉ.

1. The Gecko original tail is made up of numerous (about thirty) autotomy segments, separated from each other by as many hyaline septa marking autotomy or cleavage planes. Autotomy can occur voluntarily at any plane provided that the tail be held a short distance posteriorly to the point of separation. Autotomy in the Gecko is never 'spontaneous' or the result of mere alarm.

2. The structure of the original Gecko tail is described. The caudal artery develops a sphincter muscle in its walls immediately anterior to each autotomy plane as a means of avoiding haemorrhage after autotomy. I am not aware that a sphincter muscle has previously been described in connexion with a blood-vessel. The caudal vein is similarly constricted in front of each autotomy plane. The base of the tail differs from the segmented portion in the absence of fat bands and in the arrangement of the muscles. The flexor muscles of each tail segment are firmly attached posteriorly to the vertebra and the outer surface of the fat bands; anteriorly, however, they are only attached to the connective tissue of the hyaline matrix in the autotomy plane and are therefore easily separated. Autotomy is effected by the strong localized contraction of these muscles separating their weak anterior attachment.

3. Comparison of the Gecko tail with the non-autotomous tail of *Calotes* shows that in order to effect autotomy the former has become greatly simplified. The scales have become rearranged at the extremities of each autotomy segment, the superficial muscles have also become rearranged on a more simple plan, and the internal longitudinal continuous muscle

bands have degenerated into the fat bands and become secondarily segmented.

4. The autotomy planes are marked by simple septa of a hyaline matrix bordered by connective tissue, which traverse and separate into segments the entire substance of the tail. The spinal cord, nerves, and blood-vessels are, however, continuous.

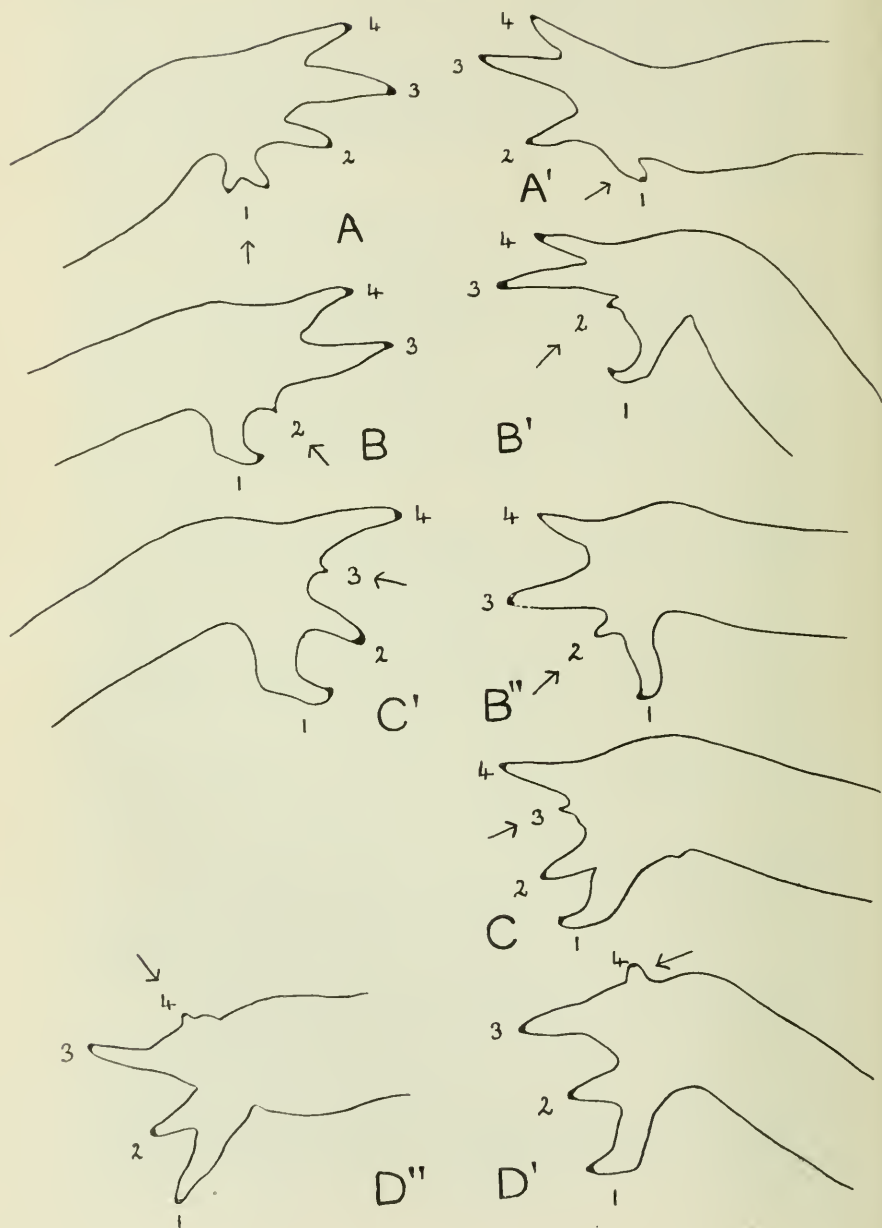
5. The structure of the regenerated tail is described. Reissner's fibre is present in the regenerated spinal cord, as in the cord of the original tail. Boulenger's explanation of the changed character of the lepidosis of the regenerated tail when compared with that of the original tail, viz. that it is a reversion to an ancestral type, does not apply to the internal anatomical features which distinguish the regenerated from the original tail. A more probable explanation of the differences between the regenerated and original tails is that the former, being merely produced for autotomy purposes, is 'jerry-built'—an appropriate description of a tail in which the muscles have no direct connexion with the endoskeleton and the spinal cord is devoid of nerves, ganglion cells, and fibres.

6. Tails of the normal regenerated type can be produced from cut surfaces situated between the autotomy planes and anterior to the first autotomy plane in the base of the tail. This is proof (a) that the histogenetic cells occur throughout the tail substance and quite apart from the hyaline septa, (b) that the peculiar features of the regenerated tail are not due to a lack of organic connexion with the rest of the body caused by the interposition of the autotomy plane septa.

7. The axis of the regenerated tail usually tends to be placed at right angles to the plane of the cut on the tail stump. In four of my experiments accessory tails were produced, none of which contained a cartilaginous tube endoskeleton.

8. The tails of *Pygopus* and *Lacerta viridis* are apparently almost identical in structure with those of the Gecko, and in *Sphenodon punctatus* the tails only differ essentially in the absence of the fat bands and the absence of sphincters on the caudal artery.

TEXT-FIG. 6.



In conclusion, I wish to express my thanks to Professor Arthur Dendy, F.R.S., for his kind gift of two tails (one regenerated) of *Sphenodon punctatus*, to Professor J. P. Hill, F.R.S., for the loan of three slides of the tail of *Pygopus* sp., to my pupil Mr. B. K. Das, M.Sc., University of Allahabad Research Scholar in Zoology, for much assistance in the practical work connected with caudal regeneration under abnormal conditions, and to Professor D. R. Bhattacharya, M.Sc., for some aid in 1914.

APPENDIX. NOTE ON THE REGENERATION OF DIGITS IN AN INDIAN TOAD.

Since, so far as I am aware, only one instance¹ has yet been described of a very limited regeneration of amputated digits having occurred in adult Anura, I reproduce here drawings (Text-fig. 6) made by my former pupil, Mr. N. K. Patwardhan, M.Sc., of regenerated digits in the Indian toad; *Bufo melanostictus*. These digits had been removed (in all cases they were cut off with scissors to a little below the level of the bases of the adjoining digits) for purposes of identification. All the figures represent the amount of regeneration which had occurred within 73 days of amputation, excepting figs. C, B",

¹ I refer to Gadow's statement (Cambridge Natural History, vol. on Amphibia and Reptilia, p. 67) that in two specimens of *Rana temporaria* in which the hand was amputated from the wrist, 'within a year this changed into a four-cornered stump and two of the protuberances developed a little further, reaching a length of about 4 mm. These specimens lived for four years without further changes.'

TEXT-FIG. 6.

Regenerated Digits of the Indian Toad, *Bufo melanostictus*, from the dorsal aspect (all figures $\times$ cir. 3).

The arrows indicate the regenerated digits. B", C, and D' (all males) represent 94 days growth; all the others (all females) 73 days growth. It is noteworthy that in A and A' the first digit has grown more rapidly than any of the other digits, though these animals were females, and the digit therefore was not used for the nuptial embrace.

and D', in which the period was 94 days. The latter maximum period of thirteen weeks, three days was therefore considerably less than the year referred to by Gadow, and in this connexion I may mention that in another toad (a toad labelled J, celebrated in its way since it was the only animal in which the renal afferent veins, each cut in two, became regenerated), in which I amputated the 5th toe on both hind legs, that on the left leg became completely regenerated within fifteen months, though that on the right leg was not re-formed to any considerable extent. Unfortunately I neglected to make a drawing of this before I left India. Figures A and A' represent the regenerated 1st digits on the left and right arms respectively, and it is noticeable that though the period of regeneration was only 73 days, and though both specimens were females (the digits therefore not being used for the nuptial embrace), yet they are better developed than any of the other digits. The other figures show the partial regeneration of the 2nd, 3rd, and 4th fingers.